A MORPHOLOGICAL STUDY OF THE UMBELLIFERAE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **298**

HILARY STANISLAUS JURICA

(WITH PLATES XIII, XIV)

Introduction

The fact that the Umbelliferae are so extensive and so well distributed throughout the northern university zone has made them an object of frequent study. CÉSALPIN (9) was the first to assemble the different members of the Umbelliferae into a separate group, not only on the basis of their umbellate inflorescence, but also on the basis of a secondary character, the two-celled ovary, each cell of which gives rise to a single seed. MORISON (51) recognized the family on the basis of the same characters as CÉSALPIN, but added a number of other plants, especially some of the Valerianaceae and *Thalictrum*, which of course, were not destined to remain within this family. To these, he applied the name of imperfect Umbelliferae. According to GÉNEAU DE LAMARLIÈRE (27), however, it was left for HERMANN (1690) to establish a rational division for this family, namely, (1) species with ovate seeds; (2) species with hairy or spiny fruits; and (3) species with large and flattened fruits. Following HERMANN, MAGNOL (27), in 1709, divided the family into four groups based on the character of the surface of the fruit: (1) fruit ribbed, (2) fruit large, (3) fruit spiny, and (4) fruit long.

The classification of the Umbelliferae entered upon a new phase with LINNÉ (45), who selected or rather borrowed from his contemporary ARTHEDIUS the row of bracts of the involucre and of the involucel as a principal character, upon which he based his division of the Umbelliferae, with the already mentioned external features of the fruit as secondary characters. At this time the essential distinction between a cyme and an umbel was not considered, and accordingly very many forms were included, which later workers, notably ADAMSON (1), CRANTZ (15), SPRENGEL (63), HOFFMANN

(32, 33), KOCH (42), DE CANDOLLE (17), etc., assigned to other families. A somewhat extensive discussion of the history of the classification of Umbelliferae may be found in the work of GÉNEAU DE LAMARLIÈRE (27). For American workers, COULTER and ROSE (13) listed a condensed bibliography of all the works containing new names or new descriptions of Umbelliferae found within the North American range, from LINNAEUS' *Species Plantarum* (1753) to that of CONGDON (1900).

The first morphological work of note upon the Umbelliferae was that of TITTMANN (65), whose figures showed the germination of some species with great exactness. Influenced by the research work of their age, or at times by the somewhat peculiar nature of the plant at hand, a further study of the germination of a large number of genera and species was made by DE CANDOLLE (17), TREVIRANUS (69, 71), BERNHARDI (4), KIRSCHLEGER (40), IRMISCH (36, 37), VAN TIEGHEM (76), GÉNEAU DE LAMARLIÈRE (24, 25, 26, 27), DOMIN (18), DRUDE (20), HOLM (35), and MÖBIUS (49).

Although DE CANDOLLE (16) had already described the stem of *Ferula*, whose medullary bundles could easily lead one to mistake it for a monocotyledon stem, it was left for HOFFMANN (34) to present us with the first extensive anatomical work upon the Umbelliferae. His study of the roots of the plants of this family contains many interesting details, but it is to be regretted that he failed to distinguish the root from the rhizome, and at times even confounded it with the lower part of the aerial stem. Moreover, he paid no attention to order and very little to development.

Further anatomical studies were made by JOCHMANN (38), REICHARDT (58), DUCHARTRE (21), BEHUNECK (3) FAURE (22), GERARD (28), TRECUL (68), COURCHET (14), HOLM (35), KLAUSCH (41), GÉNEAU DE LAMARLIÈRE (27), NOENEN (55), and NESTEL (54). The work of MÖBIUS (49), however, deserves special attention, for the parallel-veined leaves of numbers of species of *Eryngium*, together with the general aspect of their gross morphology, lead many taxonomists to suspect an analogy in their anatomy to that of some of the monocotyledons. Accordingly, we have species like *Eryngium yuccifolium* Michx., *E. bromeliaefolium* Delar., *E. pandanifolium* Chan., *E. luzulaefolium* Chan., *E. junceum* Chan.,

and *E. scirpinium* Chan. In his extensive work covering the anatomy of the leaf, stem, rhizome, and root, MÖBIUS showed that this similarity is only apparent, and that in reality the stem of *Eryngium* is not merely a dicotyledon, but is one of an advanced type.

A rather unique and quite extensive study of the mechanical tissue in the stem and leaf was made by FUNK (23), as recently as 1912.

The formation of the leaves, umbels, and gross morphology next received attention from workers like JOCHMANN (38), BUCHENAU (7), MOHL (50), ROSSMANN (60), CLOS (10, 11), GERARD (28), KLAUSCH (41), DOMIN (18, 19), PETERSEN (57), RENNERT (59), TERNETZ (66), WRETSCHKO (84), and GRIESEBACH (29).

The oil ducts or secreting canals were studied by MEYEN (47), JOCHMANN (38), MEYER (48), VAN TIEGHEM (73, 74, 75), MÜLLER (53), MOYNIER DE VILLEPOIX (52), LANGE (43), and VUILLEMIN (79).

PAYER (56), TRECUL (67), and JOCHMANN (38), whose works appeared but a few months apart, were the first to attempt the organogeny of this family. In the formation and development of the leaves all three disagree, and all differ from the account given by GRIESEBACH (29), but the accounts of PAYER (56) and JOCHMANN (38) agree in regard to the floral development and also with the accounts of SIELER (62) and HANNAH (31). SIELER, however, interprets the "calycis primordium" of these workers as a special kind of organ, which gives rise to the calyx, and naturally he finds fault with the seemingly existing "primordialkelch," a view which I failed to receive from the reading of both PAYER'S and JOCHMANN'S works. JOCHMANN'S work especially evinces great care, and no doubt, had modern technique been available in his day, the embryogeny would have been included. Like all the earlier workers, JOCHMANN begins his study with germination, but, unlike them, he pays special attention to the root, rhizome, and stem, their anatomy, and their oil ducts. He then proceeds to discuss the development of the leaves, umbels, flower, stylopodium, style, "gynoecium," pericarp, and the seed.

Among other workers dealing with the development or histology of the fruit may be mentioned LANESSAN (44), BARTSCH (2),

TREVIRANUS (70), and TANFANI (64). Quite recently an approach was made to the study of embryogeny by CAMMERLOHER (8), who studied the "Samenanlagen" of a large number of genera; and MARTEL (46) presented us with an anatomy of the flower.

Summing up all the work done, however, we find that the classification, gross morphology, anatomy, mechanical tissue, oil ducts, development of leaves and inflorescences, floral development, and development of fruit in this family are well covered, but embryogeny proper, endosperm formation, and the embryo still remain to be studied. It is with a view to filling this gap that this investigation has been entered upon.

Methods

The material used in this study was collected at different intervals in the vicinity of Lisle, Illinois. The fresh material was killed in a stock solution of chromo-acetic acid, imbedded in paraffin, and stained usually with either safranin and Delafield's haemotoxylin, or safranin, gentian violet, and orange G (omitted in a few cases).

The study centers about *Eryngium yuccifolium*, with frequent comparisons with other genera, especially *Sium cicutaefolium*.

Floral development

No attempt has been made to present a study of the development of the inflorescence or umbel, for that has already been well studied by workers listed in the introduction. Nevertheless, since the umbels of *Eryngium yuccifolium* consists of distinct compact heads, a short note in regard to the head will not be out of place.

The central or apical head of each umbel develops earlier and more rapidly than the encircling members, hence by the time the central head becomes visible to the naked eye, longitudinal sections show that the encircling heads develop in the axils of the bracts subtending the umbel, in much the same manner as described by JURICA (39) for the heads of *Dipsacus sylvestris* (fig. 1).

As already has been described by JOCHMANN (38) for *Eryngium planum*, all the flowers in the heads of *Eryngium yuccifolium* arise from the axils of bracts spirally arranged. The blossoming begins

at the base and extends toward the apex (fig. 1). The individual epigynous flowers appear as an undifferentiated mass of cells, somewhat rounded at first (fig. 2), but soon broaden out, so that the individual sepal primordia forming the calyx (which is well pronounced in *Eryngium yuccifolium*) are distinctly visible (figs. 3, 4). This is soon followed by a perfect and regular acropetal succession, presenting the sequence sepals, petals, stamens, and carpels, in perfect accord with the account given by HANNAH (31) for *Sanicula marilandica;* by PAYER (56) for *Heracleum Sphondylium* (and other species of *Heracleum*), *Carum*, *Aegopodium*, *Anethum*, *Phellandrium aquaticum*, etc.; and by SIELER (62) for *Heracleum*, *Sphondylium*, *Chaerophyllum bulbosum*, *Cicuta virosa*, *Daucus Carota*, *Peucedanum cervaria* Lat., *Angelica sylvestris*, etc. (figs. 2–7). It is well to note, however, that SEILER (62) is more concerned with the study of the sequence of the appearance of individual members within a cycle than with the sequence of the cycles themselves.

JOCHMANN (38) had noted that, although the calyx primordia make their regular appearance in *Aegopodium*, etc., they fail to continue in their development ("in pristino statu remanent, et quo, magis flos accrescit, eo magis evanescunt"), and thus apparently simply remain as calyx teeth, and in many genera even these are obsolete and hardly distinguishable (figs. 9, 10).

Ovules

The carpels are distinctly two in number at first, but soon unite along their inner face, so that in cross-section they appear to be semicircular (fig. 7); or as PAYER (56), JOCHMANN (38), SEILER (62), and CAMMERLOHER (8) would have it in the forms studied by them, "semilunar" in shape. In each of the four free ends of the coalesced carpels an anatropous ovule begins to develop (figs. 11, 12), one of which soon stops, however, while the other continues in its normal development. This results in a hanging anatropous ovule, with the raphe turned inward and the micropyle outward (fig. 14). This seems to be quite general for the entire family, for it has been found in all the species studied, and it is in accord with the account of CAMMERLOHER (8), who studied the "Samenanlagen" in thirty-seven genera and forty-five species. Moreover, JOCHMANN

(38), PAYER (56), and SEILER (62) have noted it in their work. Nevertheless, it is not out of place to note that, in one exceptional case, all the flowers of one head of *Eryngium yuccifolium* developed two normal ovules in each ovary cavity (fig. 13).

Megaspore and embryo sac

By the time the ovule has reached the stage shown in fig. 17, the nucellus has become quite prominent, and the hypodermal archesporium is easily recognizable (fig. 18). This figure shows the megaspore mother cell nucleus in synapsis, which indicates that the reduction division is about to occur. The successive stages in the development of the megaspore, resulting in a linear row of four megaspores (fig. 19), as well as the destruction of the potential megaspores, present no essential deviations from the process as ordinarily described, for the embryo sac develops from the innermost megaspore, and *Sium cicutaefolium* is no exception in this case (figs. 15, 16). The nucellus has only a single layer of cells surrounding the megaspore, but the absence of tapetal cells is well compensated by the presence of a nutritive apparatus (figs. 16, 20–25) in the chalazal region. The nucellus undergoes but slight development, and then begins to break down (figs. 16, 21–25). Even in the development of the embryo sac there is nothing unusual. The megaspore nucleus divides by three successive divisions, and at first an eight-nucleate, and then a seven-nucleate embryo sac is the result. The amount of protoplasm in the developing sac is comparatively small, frequently resulting in the presence of very large vacuoles, not only in the embryo sac proper, but in the synergids and oosphere as well (figs. 23–25). The antipodal cells, three in number, can easily be seen in the embryo sac before the polar nuclei fuse, and generally are arranged in the form of a triangle (fig. 24). They soon break down, however, and only rarely can be distinguished at a later stage (fig. 16), that is, they are somewhat ephemeral, breaking down shortly before or after the fusion of the polar nuclei.

Endosperm and embryo

Shortly after double fertilization the endosperm nucleus begins to divide, forming an endosperm consisting of free nuclei (figs. 26,

27). The early divisions of the endosperm nuclei occur more rapidly than those of the embryo, and very soon cell walls make their appearance. Even after the formation of cell walls, the endosperm continues to form so rapidly that when the seed is mature the small, insignificant, yet massive embryo (figs. 28–30) is practically inclosed in rich endosperm tissue. In its development the embryo does not always divide into regular octants (figs. 28–30), but at times is quite irregular. Very frequently in its early development it looks more like a pteridophyte embryo (fig. 28), and is characterized by a long suspensor.

Relationships

The Umbelliferae are very closely related to the Araliaceae and Cornaceae, with which families they form an alliance or order known as the Umbellales, or the "Umbelliflorae" of ENGLER. Although several workers, notably HALLIER (30), WETTSTEIN (83), and WERNHAM (82), have elaborated various tables showing the probable phylogenetic relationships, the scheme of ENGLER is still followed by most workers. In ENGLER's classification the dicotyledons are divided into two great divisions, the Archichlamydeae and Sympetalae, which, according to COULTER and CHAMBERLAIN (12), however, show no sharp distinction, for "sympetalous forms occur among the former, and polypetalous forms among the latter." The distinction is laid principally upon a single character, namely, apetaly or polypetaly for the Archichlamydeae, and sympetaly for the Sympetalae. Without doubt this is pressing a single character too far, and as a result the Umbellales "stand so stiffly apart from other Archichlamydeae as to raise the question whether they do not really belong among the higher Sympetalae" (12).

It will not be out of place to indicate such evidence as there is for such an assumption from the taxonomists' point of view. For this purpose the recent extensive work of VIGUIER (78) may be cited. In his chapter dealing with the relationship of the Araliaceae with other families, he definitely proves the close relationship of the three families forming the order Umbellales, claiming, for example, that the only character which separates the Araliaceae from the Umbelliferae is the drupaceous fruit of the former, whereas the two

families have a number of general characters in common. He also states that not a single anatomical character permits an absolute separation of the two families. After describing the details of this anatomical relationship, he concludes that the Umbelliferae, with the Araliaceae, form a continued morphological series and a very natural group. VIGUIER next shows that the Cornaceae are closely related to the Araliaceae, claiming that even good systematists at times take a single genus out of one of the families and put it into another. WANGERIN (80) and WARMING (81), however, would separate the Cornaceae from the Umbellales on account of the nature of the ovule. No less apparently conclusive is the account of WETTSTEIN (83) in regard to the inter-relationship of the three families forming the Umbellales.

With this inter-relationship established, we can safely return to VIGUIER (78), who compares the Pittosporaceae with the Umbelliferae and Araliaceae on the basis of the presence of secreting canals, for which reason VAN TIEGHEM (77) has added this as a fourth family of the order Umbellales, and his studies upon the ovule of the Pittosporaceae confirm his view.

This interpretation seems plausible, for the ovary of the Pittosporaceae is likewise bicarpellate, although the ovules themselves are free and generally parietally arranged in two rows. The single integument, and the fact, as WETTSTEIN (83) has it, that the corolla is very often somewhat sympetalous ("Korolle manchmal etwas sympetal"), prove that at any rate the Pittosporaceae are out of place among the Rosales, and no doubt belong among the Sympetalae. The inclusion of the Pittosporaceae in the Umbellales by VAN TIEGHEM likewise demands the transfer of the entire Umbellales to the sympetalous dicotyledons. Accordingly they are not to be viewed as an order closing up the Archichlamydeae line, the next of kin to the Myrtales. This is in spite of the fact that the Umbellales have some characters in common with some of the Myrtales, especially with *Hippurus* of the Haloragidaceae, such as epigyny, single integument, etc., for they stand too sharply apart from the rest. The position of families forming the order Myrtales certainly deserves a reconsideration, and this has already been done in part by SCHINDLER (61), who

separated *Hippurus* from the Haloragidaceae on the basis of its morphological characters, and made a new family entitled Hippuridaceae. Further rearrangement no doubt will follow later, when more morphological work has been done on the group.

Viewing the Umbelliferae from a morphological standpoint, it is clear that separate petals are the only character which they have in common with the Archichlamydeae, and they even lack sympetaly, if the Umbellales are taken as a whole on the basis of VAN TIEGHEM'S work on the Pittosporaceae; for, according to BESSEY (5), "one organ may be advancing while another is retrograding."

"The complete cyclic arrangement of floral members associated with definite numbers" (12), the single integument (fig. 17), the anatropous ovule (fig. 14), the absence of parietal tissue of the megasporangium (fig. 18), the small nucellus (fig. 18), and the complete tetrad of the megaspores (fig. 19) of the Umbelliferae, all of which are general characters of Sympetalae in contrast with those of the Archichlamydeae, from which the Umbelliferae stand so stiffly apart, prove that the Umbellales in reality belong among the Sympetalae.

The question now arises, if they are to be placed among the Sympetalae, what is their relative position? This is not difficult to answer, for the epigynous nature of their flower places them surely above the Tubiflorales, and their other floral characters put them below the Campanulales. Hence, a position in the neighborhood of the Rubiales is without question. C. E. BESSEY (5), E. A. BESSEY (6), and WETTSTEIN (84) consider the Umbellales as giving rise to the Rubiales. WERNHAM (82) notes that "within both cohorts," as he calls them, "the progress from polycarpellary to a bicarpellary gynoecium is observable; in both the ovary is only very rarely unilocular; and in both the androecium is primitively isomerous with the corolla, and the latter primitively regular." Accordingly, he recognizes the "Umbelliflorae as the representatives of a side branch from the calycifloral (rosalium) plexus, and the Rubiales as another such side branch of this stock." All this is to fit in with his scheme of a polyphyletic origin of the Sympetalae.

On the other hand, HALLIER (30) would have a common "Umbellifloren" stock reaching from the Terebinthaceae, and giving rise to Cornaceae, and through these to two branches, namely, to Umbelliferae on one side and to Rubiales on the other. From this it is evident that, although these systematists disagree as to details, they agree upon the fact that the Umbellales are related to Rubiales. Recognizing ENGLER'S scheme of classification as the one more commonly and more widely accepted, and in view of the numerous facts, both from the taxonomic and morphological field, I suggest that the Umbellales be placed among the Sympetalae parallel with the Rubiales. Even if the viewpoint of WANGERIN (80) and WARMING (81) in regard to the Cornaceae should be proved to be correct and universally accepted, this would not affect the remaining families of the Umbellales, for then the Cornaceae would be transferred to a position in close association with the Caprifoliaceae.

Summary

1. The floral development shows an acropetal succession of floral cycles, namely, sepals, petals, stamens, and carpels.

2. In the genera in which the sepals are represented by mere calyx teeth or are obsolete, the calyx primordia also make their appearance, but fail to develop any further.

3. The carpels are two in number and later fuse to form the ovary.

4. Two anatropous ovules begin to develop in each cavity, but usually the lower one reaches maturity.

5. The hanging anatropous ovule has a single integument.

6. The nucellus is very small, and the hypodermal archesporial cell is easily recognizable.

7. The megaspore mother cell produces a perfect linear tetrad, as a result of two successive divisions.

8. The embryo sac develops from the innermost megaspore, the three others aborting.

9. A regular eight-nucleate and subsequent seven-nucleate embryo sac results from three successive divisions of the megaspore, followed by the fusion of the polar nuclei.

10. The antipodals are somewhat ephemeral, breaking down either shortly before or after the fusion of the polar nuclei.

11. The endosperm nucleus is the first to divide after double fertilization, and for a while continues to produce free nuclei, but cell walls soon appear.

12. The fertilized egg is slow to divide, and undergoes no extensive development, so that the ripe seed has a small embryo imbedded in rich endosperm tissue.

13. The suspensor is somewhat long.

14. The morphological features of the Umbelliferae show that they are out of place among the Archichlamydeae, and that they belong among the Sympetalae, in spite of their separate petals, just as *Agapanthus* is a good monocotyledon in spite of its two cotyledons.

15. The epigynous nature of the flower in close affinity with that of the Rubiales warrants the placing of the Umbellales about parallel with the Rubiales, among the Sympetalae, that is, as a side line having a common origin with the Rubiales.

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ST. PROCOPIUS COLLEGE
LISLE, ILL.

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EXPLANATION OF PLATES XIII, XIV

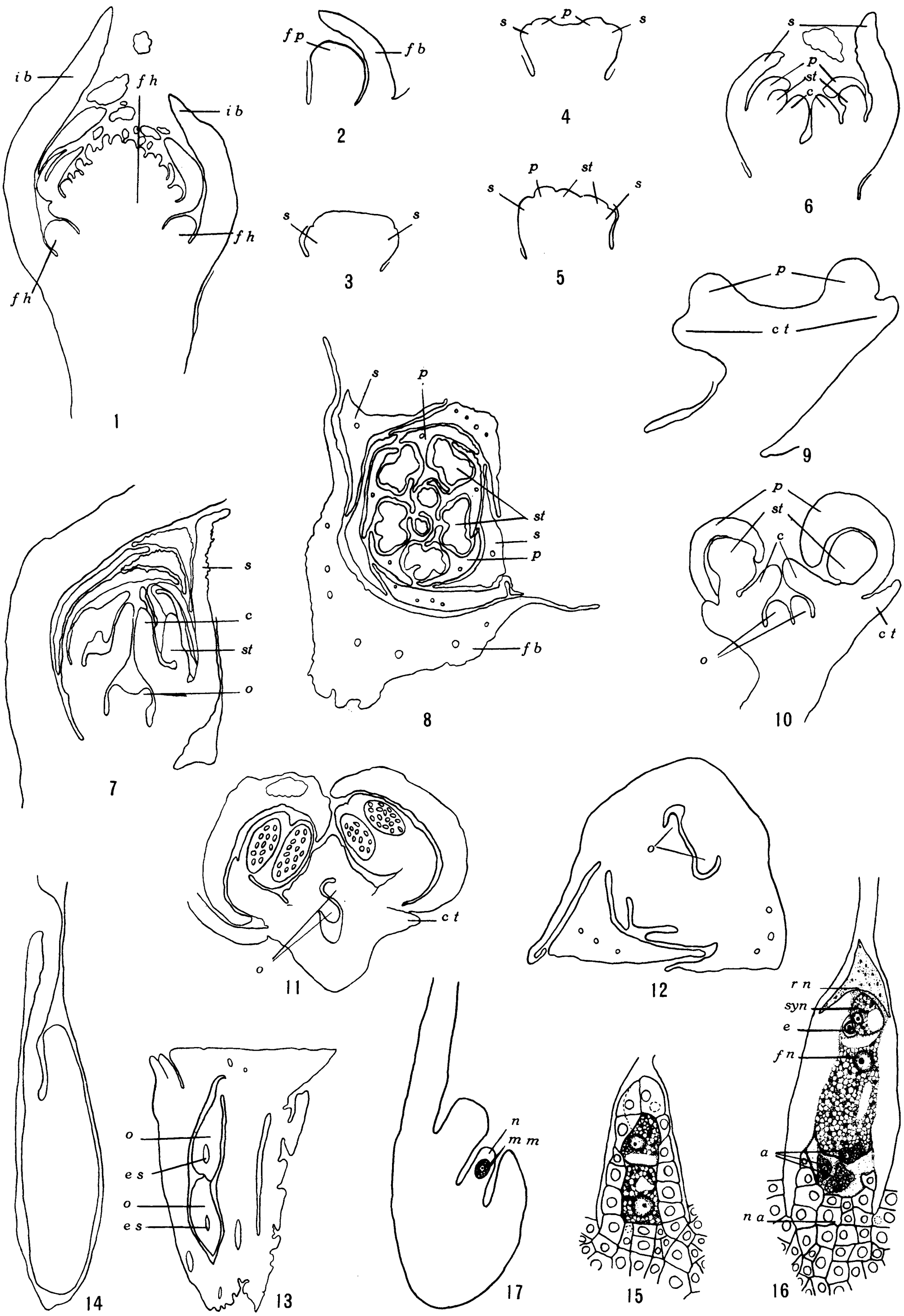
Abbreviations: *fh*, floral head; *ib*, involucral bract; *fb*, floral bract; *fp*, floral papilla; *s*, sepal; *p*, petal; *st*, stamen; *c*, carpel; *ct*, calyx tooth; *o*, ovule; *es*, embryo sac; *mm*, megaspore mother cell; *m*, megaspore; *rn*, remains of nucellus; *na*, nutritive apparatus; *pn*, polar nucleus; *a*, antipodals; *ra*, remains of antipodals; *fn*, fusion nucleus; *e*, egg; *syn*, synergids.

FIG. 1.—A central head of *Eryngium yuccifolium*, showing origin of lateral heads composing umbel.

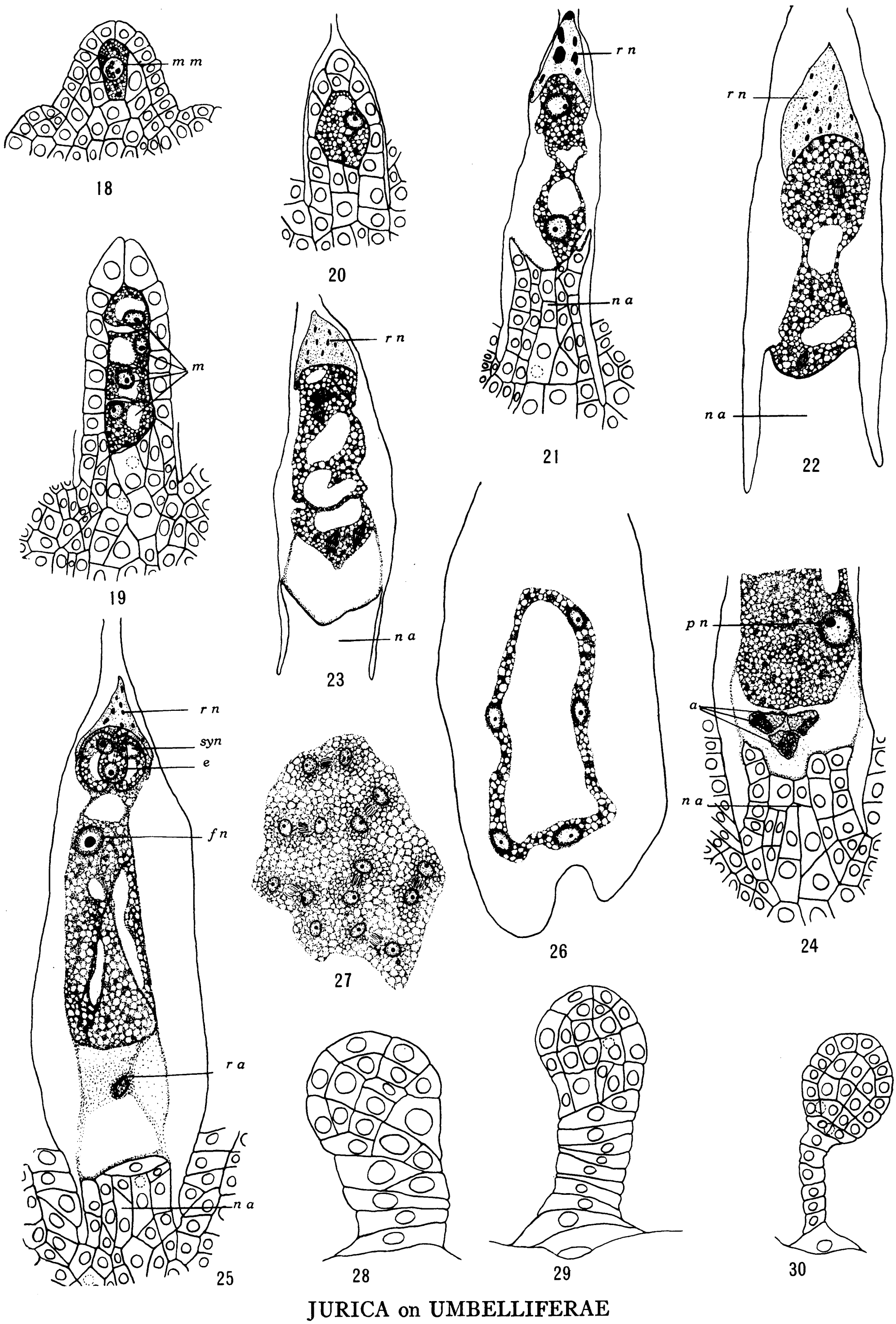
FIGS. 2–7.—Stages in floral development of *E. yuccifolium*.

FIG. 8.—Single mature flower of *E. yuccifolium* in cross-section, showing arrangement of floral cycles.

FIGS. 9, 10.—Stages in floral development of *Zizia aurea*, especially showing calyx teeth.



JURICA on UMBELLIFERAE



JURICA on UMBELLIFERAE

FIG. 11.—Longitudinal section of ovary of *Sium cicutaefolium*, showing the two ovules beginning development in one of ovary cavities.

FIG. 12.—Section of *E. yuccifolium* ovary, showing the two ovules in single ovary cavity; only lower ovule generally develops.

FIG. 13.—Longitudinal section of ovary of *E. yuccifolium*, showing an unusual condition, the developing of two ovules in single ovary cavity.

FIG. 14.—Anatropous ovule of *E. yuccifolium*.

FIG. 15.—Nucellus of *Sium cicutaefolium*, showing two cells, result of first division of megaspore mother cell.

FIG. 16.—Mature embryo sac of *S. cicutaefolium*, showing breaking down of nucellus, egg, one of synergids, fusion nucleus, three antipodals, and nutritive apparatus.

FIGS. 17–30.—*Eryngium yuccifolium*.

FIG. 17.—Ovule showing single integument and nucellus.

FIG. 18.—Nucellus showing megaspore mother cell in synapsis.

FIG. 19.—Nucellus showing four megaspores.

FIG. 20.—Single megaspore from which embryo sac will develop; nucellus beginning to break down.

FIG. 21.—Two-nucleate embryo sac, showing nutritive apparatus.

FIGS. 22, 23.—Two and four-nucleate embryo sac, showing nuclear divisions.

FIG. 24.—Lower end of embryo sac, showing one of polar nuclei, three antipodals, and nutritive apparatus.

FIG. 25.—Mature embryo sac, showing remains of broken down nucellus, egg, synergids, fusion nucleus, remains of antipodals, and nutritive apparatus.

FIG. 26.—Embryo sac in cross-section, showing endosperm formation by free nuclei.

FIG. 27.—Free nuclei of endosperm of embryo sac in longitudinal section.

FIGS. 28–30.—Embryo and suspensor.